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Beetle species diversity in the Lesser Antilles islands: How many species are really there?

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Abstract. Recent extensive and intensive field work by the team of M. A. Ivie on the Lesser Antillean island of Montserrat suggests that a mean of 827 beetle species may be expected on that island. This datum makes possible the generation of hypotheses of the probable beetle species diversity on other islands of the Lesser Antilles as a function of the areas of the islands. Figures are given for the presently known, estimated total, and estimated number of unknown species for each principal island. This predicts that many hundreds (if not thousands) of beetle species remain to be discovered. This is of importance to land management and conservation interests on these rapidly changing and ecologically fragile islands.

Introduction

The West Indies are recognized as one of the world's 34 "hotspots" of species biodiversity and endemism (Mittermeier et al. 2005, Myers et al. 2000). Most of the available diversity information is for vascular plants and terrestrial vertebrates. Very little published information is available for most groups of insects. The chain of islands known as the Lesser Antilles is a distinct biogeographic subregion of the West Indies (Fig. 1). Beetles represent about one out of every five animal species. I have been working towards summarizing known and new information on the beetles of the Lesser Antilles for some years (Peck 2006, 2009).

It is now apparent that the diverse fauna of beetles of the Lesser Antilles is remarkably poorly known. But a measure of our relative ignorance has not been previously available. Through the remarkable work of M. A. Ivie and his team on the island of Montserrat, an island with an area of 104 km^2, there is now a measure by which it is possible to make a hypothesis of the total beetle species numbers on other islands of the Lesser Antilles.

Methods

In 2000 Ivie et al. (2008) initiated a study of the terrestrial arthropods of the island of Montserrat following the extensive eruptions of Soufriere volcano. Ninety-four beetle species were known to occur on Montserrat at the start of the project. After an intensive and long-term study of the island, mostly in the Centre Hills, they found 718 beetle species (Ivie et al. 2008). With data on the number of species known from only one or two specimens they used the Chao-1 estimator (Chao 1984, Colwell 2005) and calculated that the actual mean expected number of beetle species on the island was 827 (with a 95% CI of 792-876). Using that estimate, Ivie et al. (2008) predicted the total numbers of some insect and other arthropod orders which may be expected on the island.

The estimate of actual species numbers of beetles can now also be used as a basis for an estimate of the species numbers of beetles on other islands in the Lesser Antilles relative to the areas of those islands. Darlington (1957) noted that within a given region of relatively uniform climate there exists an orderly relation between the size of a sample area and the number of species found in that area. He proposed, as a "rule of thumb," that as island area changes by a factor of 10, the species number changes by a factor of 2.

Darlington's rule of thumb was formalized by MacArthur and Wilson (1967), who formulated a general first approximation of species diversity in relation to an island's area to be $S = CA^z$; where S is species number, C is a constant that varies according to taxon and biogeographic area, A is island area, and z is a constant which usually varies between 0.20 and 0.35. This formula can be used to estimate the number of beetle species on other islands relative to that of Montserrat. The species-area data for Montserrat are

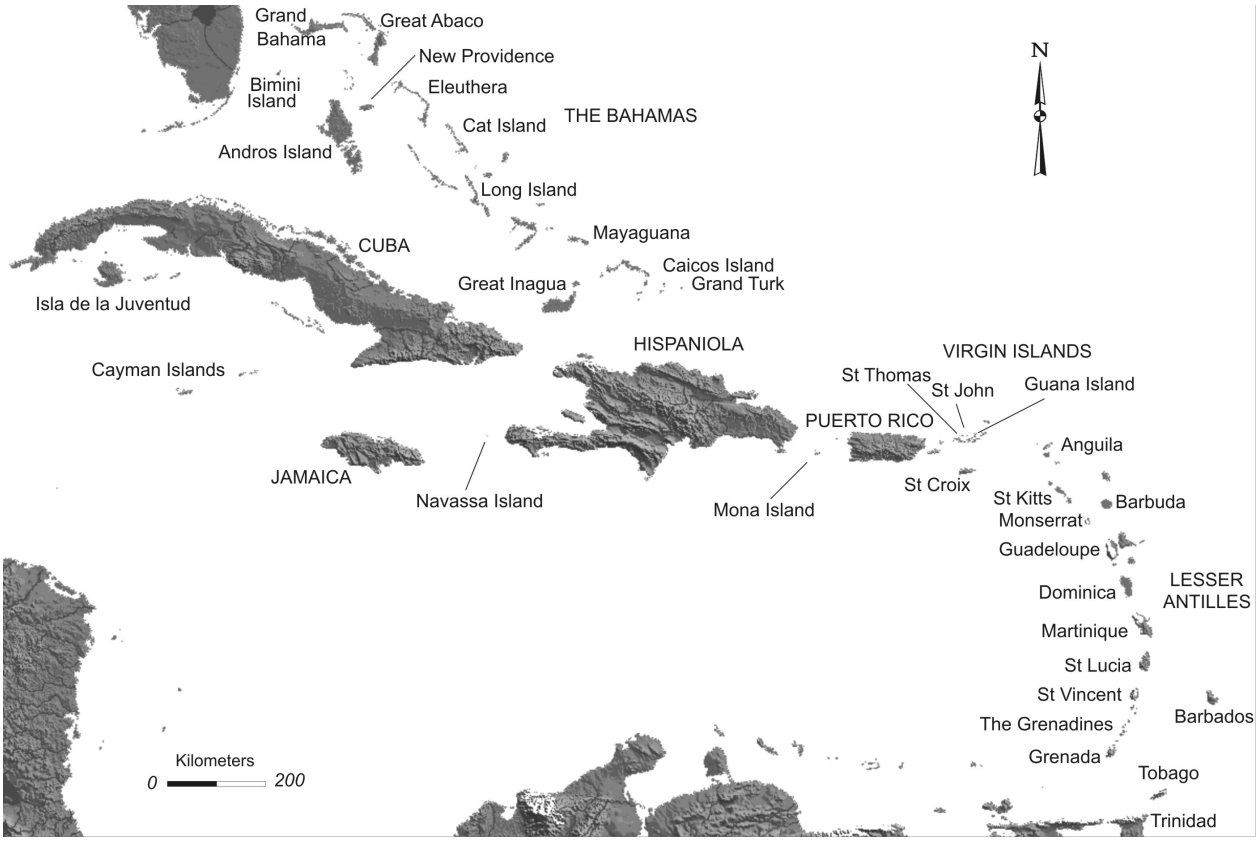

Figure l. The West Indian Biodiversity Hotspot. The islands of the central and eastern West Indies and adjacent continental land masses, with the island arc of the Lesser Antilles in the east. The smaller islands of the Lesser Antilles are not indicated by name.

here used to fix a regression line for other larger and smaller islands of the Lesser Antilles relative to their areas. An average value was used for the slope of the regression line with z = 0.301 (McArthur and Wilson 1967). From this line a hypothesized species number can be obtained for each island.

Independently, I have surveyed the literature for published records of presently known beetle species on each island in the Lesser Antilles. Blackwelder (1944-1957) was used for records preceding 1944, and The Zoological Record was used for records from 1944 to present.

Results

Figure 2 shows the regression line for the estimated change of beetle species numbers with change in island area. Montserrat fixes the line as the reference datum point. Where an island's area intersects the regression line is the hypothesized natural saturation number of species which could be on the island. Note that the available data for the other islands of the Lesser Antilles all fall below this line.

Table 1 lists the principal islands of the Lesser Antilles and summarizes their areas, elevations, known and expected beetle species numbers, and the predicted number of species yet to be discovered. The difference between each island data point and the regression line is the predicted number of species remaining to be discovered. The islands of Mustique, Grenada, and Guadeloupe are closest to the line, which suggests that they have been better sampled but are still relatively unknown. Of course, these data are estimates of total species diversity on each island, but it is not possible at present to identify what percentage of each island's fauna is endemic.

Discussion

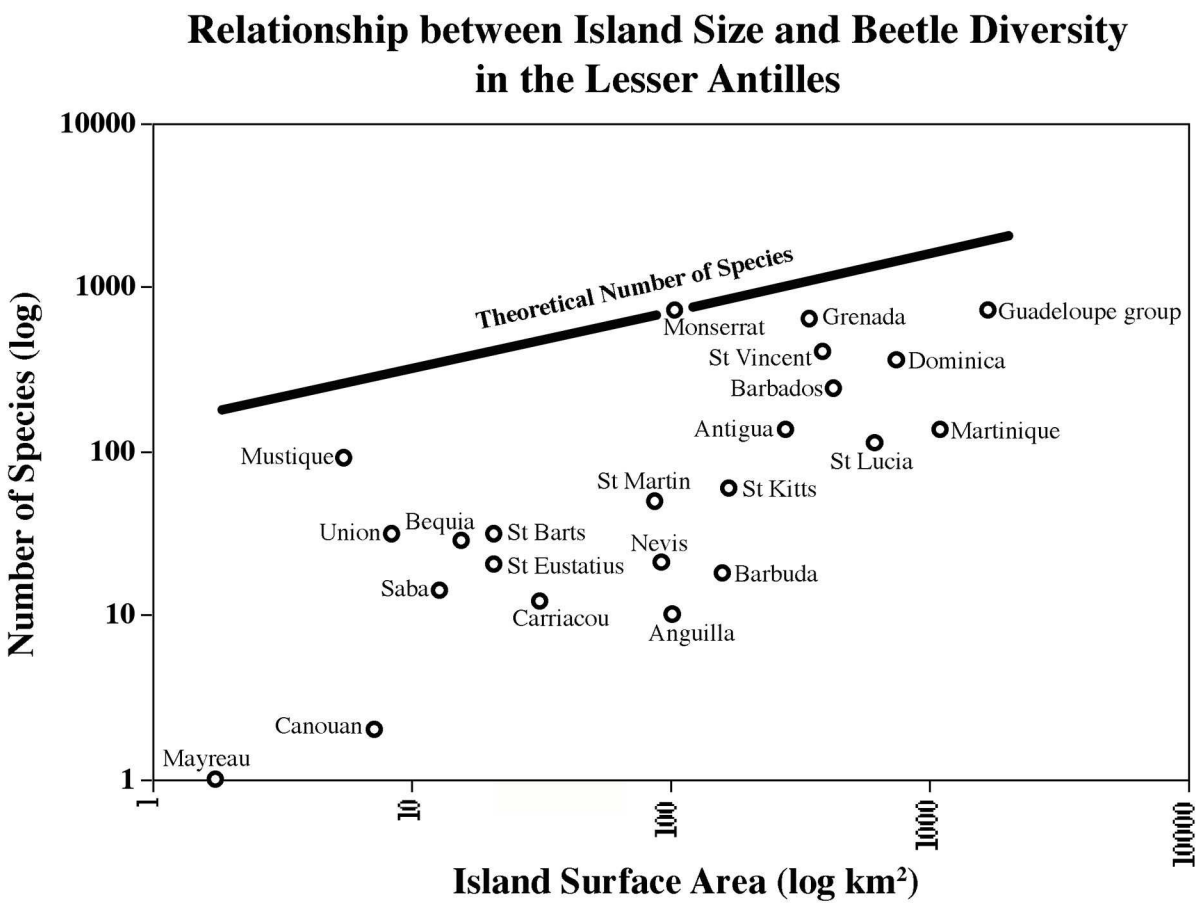

Figure 2. A theoretical relationship between increasing island area and the increase in beetle species which should be on individual islands in the Lesser Antilles. Data points are for present day island areas and published species records. The regression line slope with a z value of 0.301 indicates a natural saturation number of species which could be expected to occur on an island of a designated area. The line is anchored on the island of Montserrat, which, through the work of Ivie et al. (2008), is the only well-known island in the Lesser Antilles. The difference between the regression line and a datum point suggests how many additional species might be expected with a complete knowledge of each island's fauna.

Ivie et al. (2008) discuss the general inadequacies of knowledge of West Indian beetles. There are many variables besides island area which affect species numbers on islands, most notably island age and island elevation (Rickleffs and Lovette 1999). The only other comparable survey to consider these variables and their effect on beetle species on tropical oceanic islands is that of Peck (2005) for the Galapagos Islands.

The islands of the Lesser Antilles were formed in the Tertiary as an arc where the eastern margin of the Caribbean geological plate overrides the subducting Atlantic geological plate (Donnelly 1988). Thus, the islands have generally similar geological origins and ages, but different individual erosional, depositional, and volcanic histories, and they vary greatly in elevation, habitat diversity, and proximity to continental faunal source areas. They also have varying histories and intensities of human occupation, habitat alteration, and introduction of non-native species. All of these will modify the beetle species numbers formerly or now actually present or recoverable on each island. Nevertheless, the species diversity hypotheses are realistic estimates because they are based on data and biological principles. And they are testable by additional field work and taxonomic study.

In reality, the estimates may be too low. Valentine and Ivie (2005) report a total of 405 beetle species from tiny Guana Island in the British Virgin Islands, with an area of only 0.30 km^2. But, the data are complicated by the fact that the island is on the Puerto Rico Bank and was connected to many other islands as a much larger land mass during the last Pleistocene low sea level, some 18,000 yBP.

Table 1. Predictions of natural saturation numbers for beetle species diversity on islands of the Lesser Antilles, based on a relationship between island size and number of species. All recorded numbers of species from the literature are from a working manuscript (Peck unpublished), except for those for Montserrat (Ivie et al. 2008), Dominica (Peck 2006), and Barbados (Peck 2009). Hypothetical and expected species number have been rounded.

Island	Area (km^2)	Maximum Elevation (m)	Recorded number of species in literature	Hypothesized number of species	Expected number of species remaining to be discovered
Mayreau	1.76	85	1	240	**240**
Mustique	5.49	127	90	340	**250**
Canouan	7.29	267	2	370	**370**
Union	8.4	304	31	390	**360**
Les Saintes	10	309	30	410	**380**
Saba	13	887	14	440	**430**
Bequia	15.6	268	28	470	**440**
La Désirade	20	273	24	500	**480**
St. Barts	21	286	31	510	**480**
St Eustatius	22	600	20	520	**500**
Carriacou	31.6	236	12	580	**570**
St. Martin	87	484	49	785	**735**
Nevis	93	985	21	800	**780**
Anguilla	102	59	10	820	**810**
Montserrat	104	969	718	827	**109**
Marie Galante	153	150	33	930	**895**
Barbuda	161	39	18	945	**925**
St. Christopher	168	1156	59	955	**895**
Antigua	281	402	135	1115	**980**
Grenada	344	840	644	1185	**540**
St Vincent	389	1233	408	1230	**820**
Barbados	430	340	239	1270	**1030**
St Lucia	616	950	172	1415	**1240**
Dominica	751	1432	361	1500	**1140**
Martinique	1100	1397	134	1680	**1550**
Guadeloupe	1510	1467	1366	1850	**485**

Even though Erwin's (1982) perceptive use of beetles for his pioneering extrapolation of total global animal diversity to 30 million animal (mostly arthropod) species was controversial (May 1990), it was based on data, and did a great service by promoting additional intensive discussion and study. I hope that will be the effect of this contribution.

Applications and utility

The islands of the Lesser Antilles have been greatly changed in the past by clearing for agriculture and are now rapidly changing through development for tourism. This study provides a comparative base line for the study and documentation of one of the most diverse components of their terrestrial biotic richness. These estimates have important implications for species and conservation programs on these ecologically fragile islands. The estimates will be of value for land and resource management and habitat conservation purposes.

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